THERMAL RELATIONS OF FREE-LIVING ECHIDNAS DURING ACTIVITY AND IN HIBERNATION IN A COLD CLIMATE

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ABSTRACT

All twelve echidnas studied by radiotelemetric techniques in Kosciusko National Park 1987-1989 entered hibernation in early winter and woke in early or late spring. During hibernation, body temperatures fell close to those in the hibernaculum, as low as 3.7°C. Each individual's hibernation season was characterised by brief, periodic arousals to approximately 32°C. The frequency of arousals was proportional to body temperatures during the period of torpor, implying a possible correlation between metabolite accumulation and the function of arousals. Adults above 1300m hibernated for an average of 4.4 months, those at 1000m for 3.1 months, although the statistical significance was marginal. Echidnas gained weight at the rate of 7-13% per month in the active season and all animals for which there is adequate data also showed "test drops" (sensu Strumwasser 1960) prior to entering hibernation. Weight losses of 2-3% per month were typical in the hibernation season. During the active season, echidnas in this region were conspicuously diurnal, emerging mid-morning from their overnight retreats and remaining active until evening. Body temperatures showed a conspicuous daily cycle in every individual, the modal temperature of 32°C being reached during the daily active period. Overnight, body temperatures fell, commonly to 29°C but frequently lower. The daily cycling of body temperature was remarkably consistent from day to day and throughout the active season, both within and between echidnas. All individuals defended successfully against body temperatures above about 34°C, presumably relying particularly on behavioural rather than physiological means, and shade-seeking and waterbathing are identified as being important in this context. Neither daily minimum nor maximum body temperatures correlated with minimum or maximum ambient temperatures, implying good control over the daily temperature cycle. Nevertheless, occasional low temperatures were observed during the active season, either during "test drops" or when, in response to particularly foul weather, an individual might remain all day in its retreat, entering shallow torpor as body temperatures continued to fall until the onset of the following day's activity period. Heat produced as a correlate of muscular work appears to be the main source of the daily increase in body temperature to about 32°C.

Grigg, G.C., Augee, M.L. and Beard, L.A. (1992). Thermal relations of free-living echidnas during activity and in hibernation in a cold climate. Pp. 160-173 in 'Platypus and echidnas' (M.L. Augee, ed.). The Royal Zoological Society of NSW, Sydney.

INTRODUCTION

The ability to undergo periods of shallow (or even deep) torpor for short periods is well known in many birds and in some species of Insectivora, Rodentia, Carnivora, Chiroptera and Primates among the Eutheria (see Lyman 1982), as well as among four families of Methatheria; Didelphidae (*Marmosa* sp.) (Morrison and McNab 1962) Dasyuridae, Burramyidae and Petauridae (see Geiser 1988).

Until recently, the classical pattern of mammalian hibernation (sensu Hudson 1978), with an annual season of deep winter torpor punctuated by semiregular and apparently spontaneous but brief re-warmings to body temperatures typical of the summer, active season, was known only from Insectivora, Rodentia and Chiroptera among the Eutheria (see Lyman 1982).

Recent field studies have shown that the monotreme, *Tachyglossus aculeatus*, has a similar pattern, at least in the colder parts of its range (Grigg *et al.* 1989). A marsupial, too, the Burramyid *Burramys parvus*, is now confirmed as a deep hibernator, on the basis of both laboratory studies (Geiser and Broom 1991) and field studies (Broom, pers. comm.). Hence, deep seasonal hibernation is now known from all three groups of extant mammals.

The realisation of the extent of similarity between the thermal relations of echidnas in a cold climate and the classical mammalian pattern of hibernation came from a radiotelemetry study of echidnas in their natural surroundings (Grigg *et al.* 1989), refuting conclusions drawn from studies of individuals in captivity (Augee 1978). Nedergaard and Cannon (1990) have referred to the difficulty of working on hibernation and Lyman (1982) and others have discussed the fickleness which many species show about entering hibernation under laboratory conditions. It seems likely that, with wider application of radiotelemetry techniques, other marsupials and, probably, other Eutheria which are known torpidators (and some that are not) will be revealed as hibernators.

This paper presents further descriptive documentation of the thermal relations of echidnas in a cold climate, both in the active season and while hibernating. The aim is to describe the thermal relations of echidnas as fully as possible, against a background of ambient temperature and weather variables and to compare this pattern with that seen in eutherian hibernators.

MATERIALS AND METHODS

The study was conducted in Kosciusko National Park, near Jindabyne NSW (36°30'S,148°30'E), over the years 1986-1990, most intensively in 1987-1989. We aimed to monitor thermal relations in as many individuals and as intensively as possible, both at lower elevations in the Waste Point area (1000 m) in dry sclerophyll forest, and at higher elevations (1300-1800 m), above the normal winter snowline, in sub-alpine woodlands, heaths and alpine herbfields (Costin *et al.* 1979). Animals were captured serendipitously by park rangers and friends. The geography of the study area is shown in Figure 1.

In all, 12 individuals were fitted with radio transmitters, four from areas above the snowline. Their home ranges

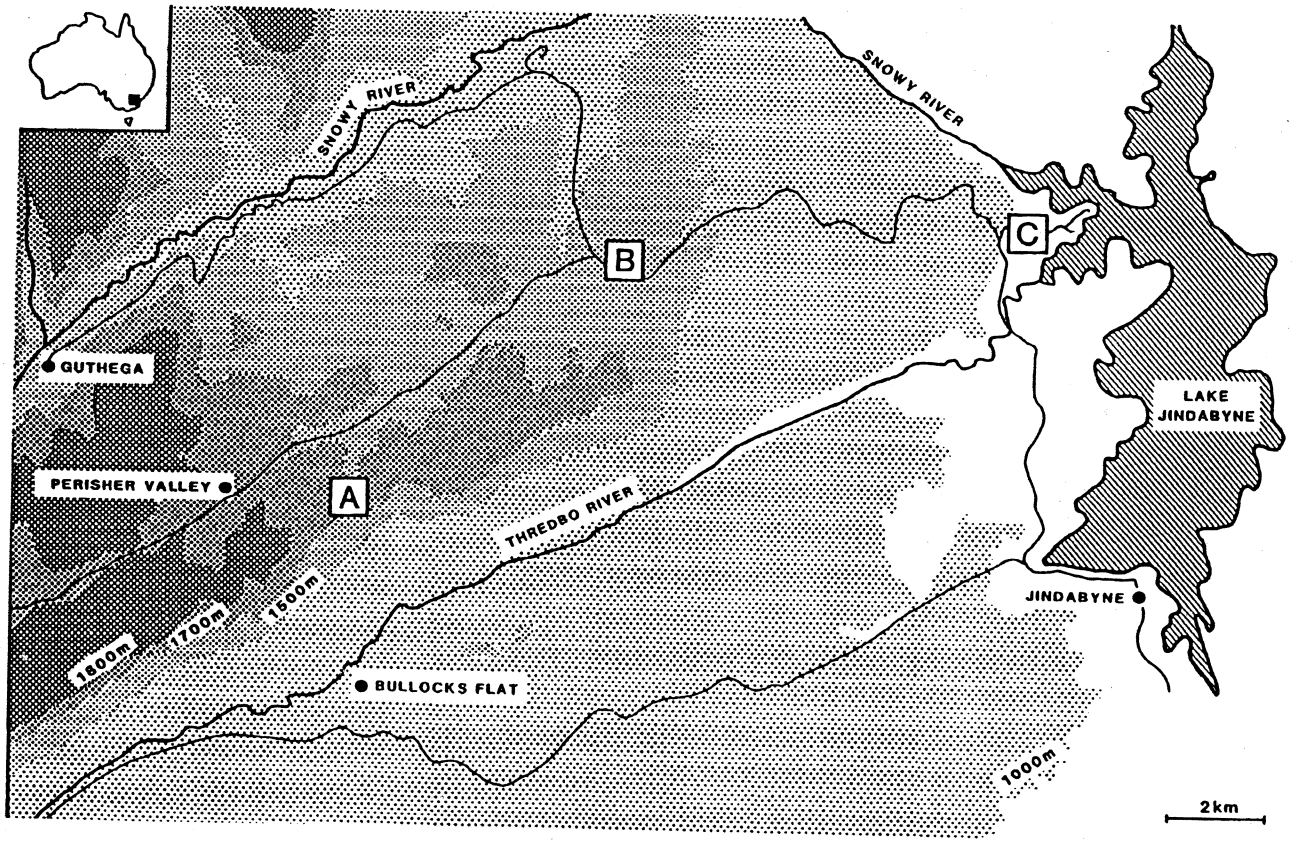

Figure 1. Map of the study area. A=Prussian Plain (1700-1760 m), alpine heath/snow gum woodland; B=Rennix Gap (1560-1600 m), alpine heath/snow gum woodland; C=Waste Point (960-1020 m), open eucalypt woodland.

are described by Augee *et al.* (this vol.). Temperature-sensitive radio transmitters (J. Stuart Enterprises, Austec Electronics or Sirtrack), calibrated against a standard thermometer, were implanted into the peritoneal cavity via a ventral mid-line incision. All surgical procedures were sterile, using Halothane as an anaesthetic and following guidelines approved by the University of Sydney's Animal Care Committee. The transmitters were potted in Elvax and were typically 60x25x20 mm (weighing about 29 gm), with a smooth rounded profile. They were sterilised in Wavicide or Aidal (Whitely Chemicals) for at least 10 minutes and then rinsed very thoroughly with sterilised physiological saline prior to implantation. To minimise stress, we released the animals soon after surgery, often within a few hours, and healing was uniformly good. Final closure of the incision was by size O surgical silk which, we found, wore through and fell out in due course, relieving us of the need to re-handle the animals to remove sutures. It was usual for us to be able to see no sign of the incision when, 6-15 months or more later, we recaptured an individual to replace its transmitter with one having fresh batteries. One individual (#11) had three different transmitters sequentially without apparent ill effect and three of the four females mated and produced young, reinforcing our confidence in the success of the technique.

All animals were released at their point of capture, except #12 which was captured at Dead Horse Gap but released at a similar altitude on Prussian Plain (36°25'S, 148°26'E) in the Ramshead Range.

We monitored radio signals either by hand, using a Telonics TR-2 receiver, or remotely, using a Telonics TR-2 receiver-scanner combination and a tape recorder turned on at pre-determined time intervals by a specially built electronic timer. Pulse intervals were determined either electronically (Telonics Digital Processor) or using a stopwatch. Ambient temperatures were recorded from similar temperature-sensitive transmitters placed at various appropriate locations, usually in soil or among leaf litter under the recording box and sometimes within a retreat or hibernaculum when that was possible.

Because of our concern to minimise the possibility of artefacts, the study animals were handled or disturbed only rarely. Hence, we have fewer body weights than would have been desirable.

RESULTS

Period of time spent in hibernation

The results in 1988 and 1989 confirmed the pattern which emerged in 1987 (Grigg *et al.* 1989). Every individual entered a prolonged period of hibernation (Figs. 2, 3). Typical patterns of body temperatures experienced by

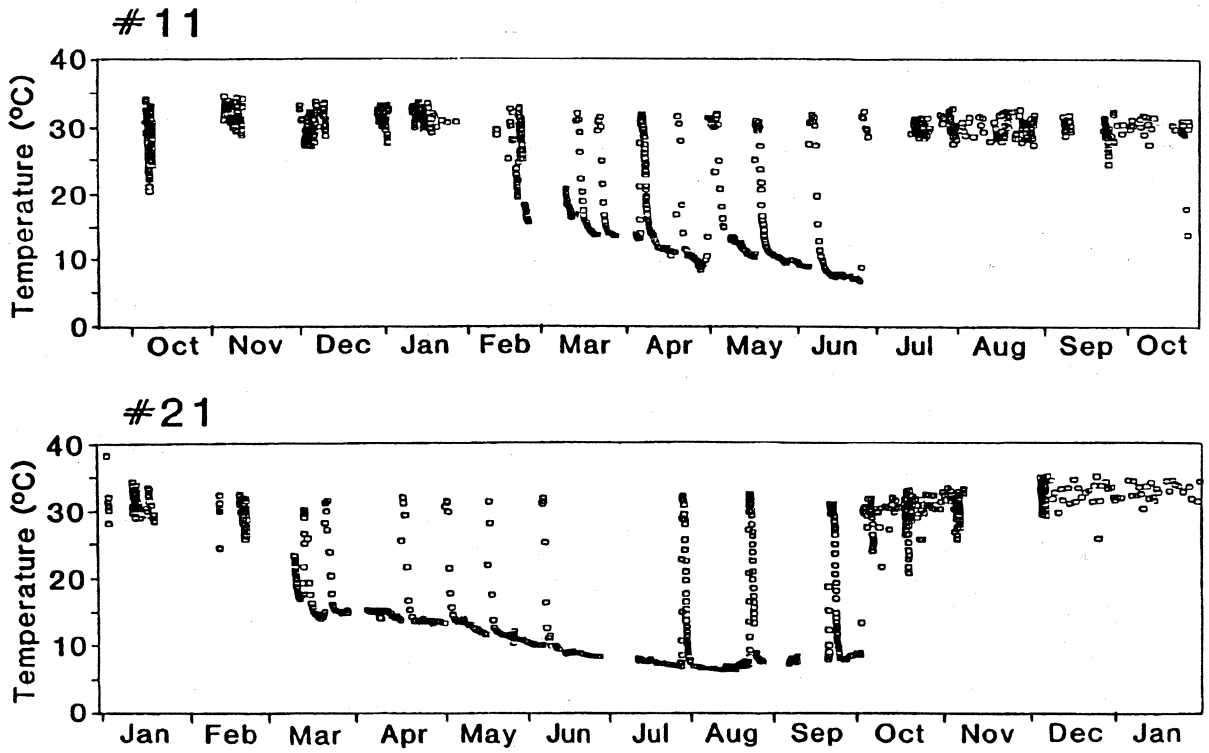

Figure 2. Annual pattern of changes in body temperatures in two echidnas monitored near Waste Point in Kosciusko National Park (upper panel = #11, Sept 1987-October 1988; lower panel = #21, Jan 1988-Jan 1989). Note the distinct hibernation season in each case. Both are males, #11 mature, #21 immature .

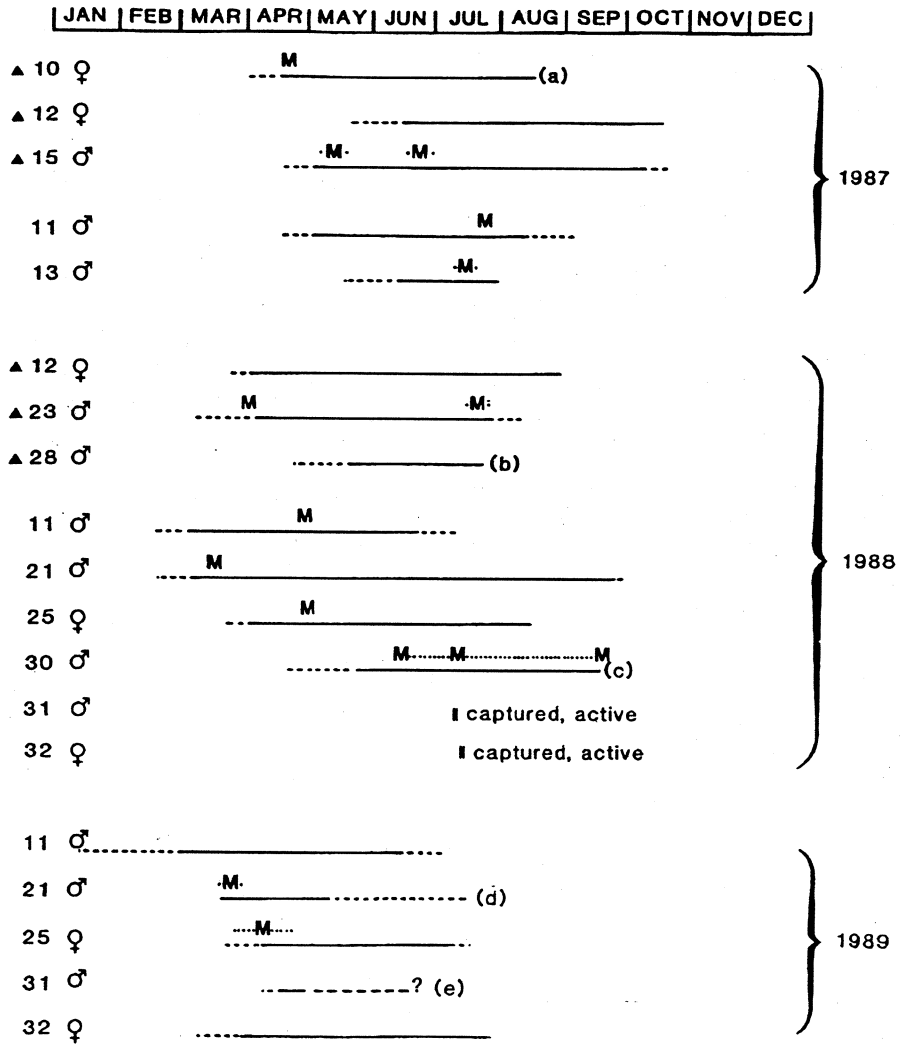

Figure 3. Schematic showing duration of hibernation (solid lines) for each echidna in the study over the years 1987 to 1989. A solid triangle identifies animals whose home range was higher than 1300m elevation, above the winter snowline. Dashed lines indicate uncertainties about exact dates of entry to or arousal from hibernation (see text). An M indicates movement to a new hibernaculum; dotted lines indicate uncertainty about when the movement occurred. Notes: (a) #10, dug out of hibernation when transmitter failed (b) #28, died in hibernation; line stops at last arousal event (c) #30, dug out of hibernation because too distant to continue monitoring (d) #21, transmitter failed; last data at end of solid line; animal not in hibernaculum at end of dotted line (e) #31, as for #21.

two echidnas are shown in Figure 2. The hibernation state was distinct in every case, an animal having abandoned its normal activity pattern with daily body temperatures in the low 30s (see below), remaining in a retreat and letting its body temperature fall close to ambient temperature. Exact entry dates could not be determined because no animals entered torpor within range of a recording box. Entry dates were, however, earlier in 1988 and 1989 than in 1987, possibly because later release of animals in 1987 may have postponed entry (see Beard *et al.* this vol.). In 1988 and 1989 all but one of the individuals (#30) had been fitted with a transmitter and released in the previous year. Hence, data from 1988 and 1989 are likely to be more valuable as an indication of the normal time of entry into hibernation in Kosciusko National Park. Even though exact entry dates are lacking, it is clear that dates are variable between individuals and that March is the month in which most entries occur. Once animals were in hibernation and were located, we continued to monitor them at their known locations so we have more accurate data about their emergences from hibernation (Fig. 3). Emergence times show considerably more variation between individuals, ranging from late June to October, and the pattern which emerges here in relation to reproduction is the subject of a paper elsewhere in this volume (Beard *et al.*). Briefly, sexually mature individuals (above 3kg, see Beard *et al.*) woke in time to mate during the normal July-August breeding season whilst immature animals commonly remained in hibernation well into the spring.

Ignoring uncertainties about the beginning and end of hibernation, minimum periods of hibernation for individuals monitored through a complete season ranged from 1.6 - 6.6 months, centred on autumn and winter (Fig. 3). The data suggest a tendency for adults with home ranges at elevations above 1300m to have a longer hibernation season (4.4 months ± sd=0.66, 5 observations from 4 echidnas) than those at 1000m (3.1 months ± sd=0.96, 8 observations from 5 echidnas), but the statistical significance is marginal ($P = 0.06$, $df = 7$) .

Hibernation was broken by characteristic periodic arousals during which normal temperatures were regained for a few hours or, sometimes, up to 24 hours. Sometimes an individual left its retreat (hibernaculum) during an arousal event and moved to another site at which it re-entered torpor. Such events, indicated in Figure 3, tend to occur

either early or late in the hibernation season. In the case of #15 and # 30, the relocation may have been associated with some form of disturbance by the investigators.

An echidna's year in Kosciusko National Park is, therefore, divided into an active season through spring, summer and early autumn and a season of hibernation which may last from 2 - 7 months. It will be convenient to describe separately the thermal relations of echidnas in each of these two activity patterns.

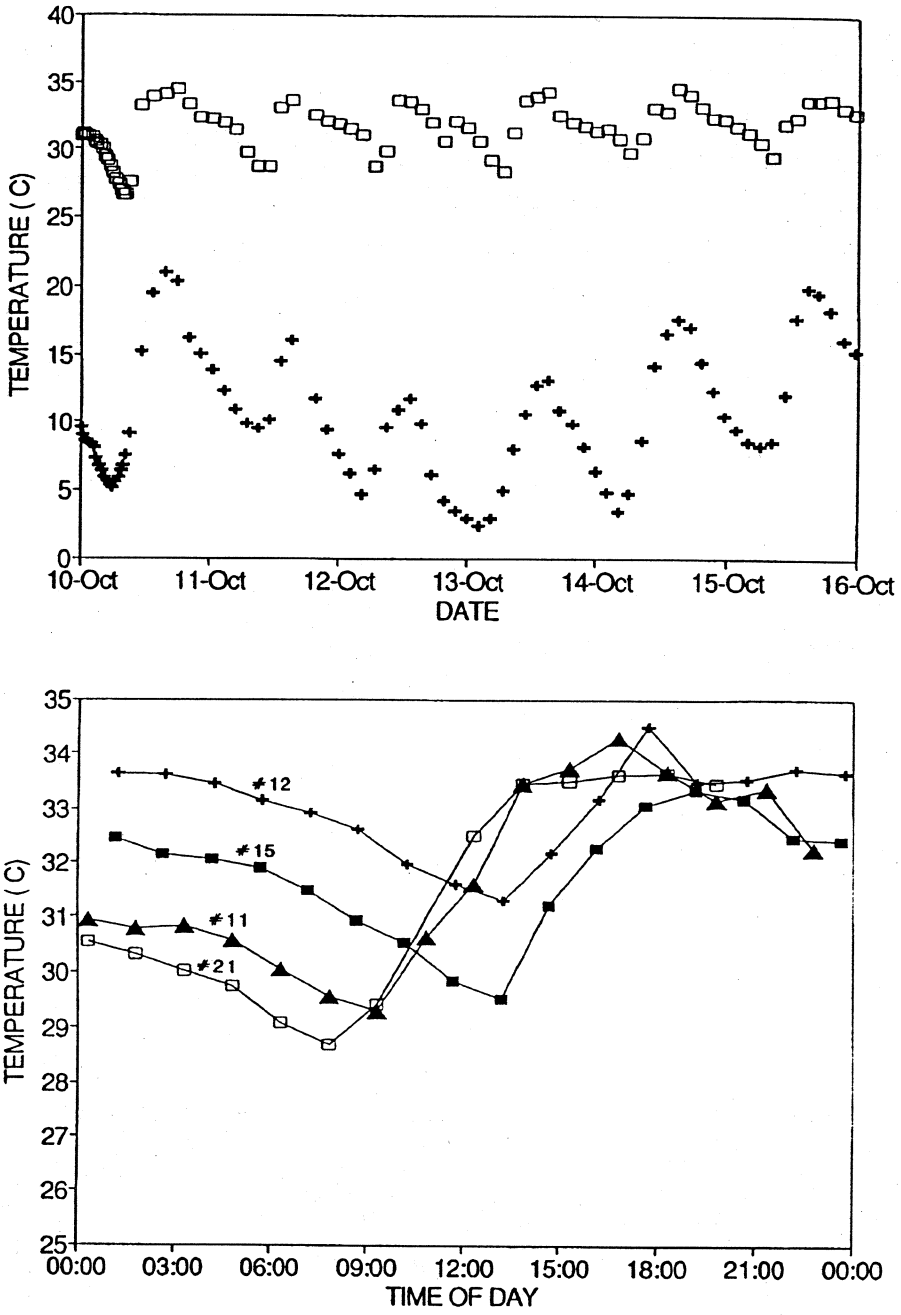

Figure 4. Typical daily cycles in body temperature in echidnas during their active season in Kosciusko National Park. Upper panel: body (open squares) and ambient (+) temperatures recorded from #21 over six days in October 1987. Lower panel: superimposed cycles in body temperature in echidnas #11, #12, #15 and #21 for 8 November 1987

Thermal relations of echidnas in their active season

All echidnas showed a pronounced daily cycle in body temperature, with minimum temperature at early-mid morning just prior to exit from the overnight retreat (Figs. 4,5,6). Typical daily patterns are shown in Figure 4. After leaving the retreat, T_b rises rapidly, correlating with the onset of foraging behaviour. Maximum T_b is reached, usually, during the afternoon or early evening. Interestingly, rather than a plateau temperature being characteristic of the period of activity, the pattern is typically more like that of a sawtooth, with maximum temperatures being seen towards the end of the active period. Once the animal enters a retreat, it cools gradually towards the next morning's minimum. This general pattern is persistent for an individual, even when data from many individuals are combined (Figs. 5 and 6). No pattern emerged correlating the times of minimum or maximum body temperatures with season. Pooling all data and plotting as a histogram, it becomes clear that echidnas defend very successfully against becoming overheated, but are far more tolerant of body cooling (Fig. 7).

On two occasions we saw individuals apparently take behavioural action to reduce overheating (Fig. 8). On a windless December day on Prussian Plain (1800 m), (T_a max = 11.2°C), the body temperature of #12 had increased gradually to 34°C as it foraged, when it abruptly moved about 20 metres to the shade of a small rocky overhang, initiating a fall of almost 2°C, some of which occurred after the animal had again resumed foraging, due, presumably, to thermal inertia (Fig. 8 upper panel). On a warmer, similarly windless January day near Rennix Gap, #15 was under observation as it

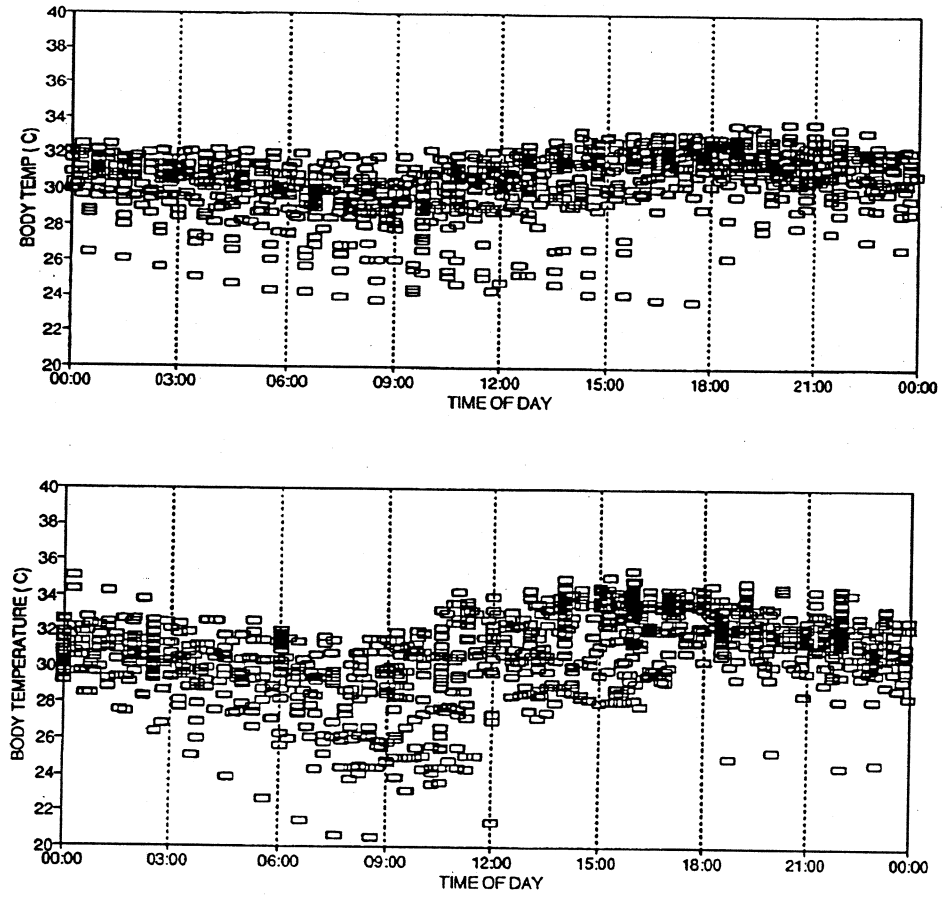

Figure 5 (LEFT). Day to day similarity of daily cycles in body temperature for individual echidnas throughout the active season, illustrated by pooling all data from #13 between August 1987 and February 1988 (upper panel) and all data for #21 between October 1987 and February 1989 (lower panel). See text for discussion of the several runs of low values.

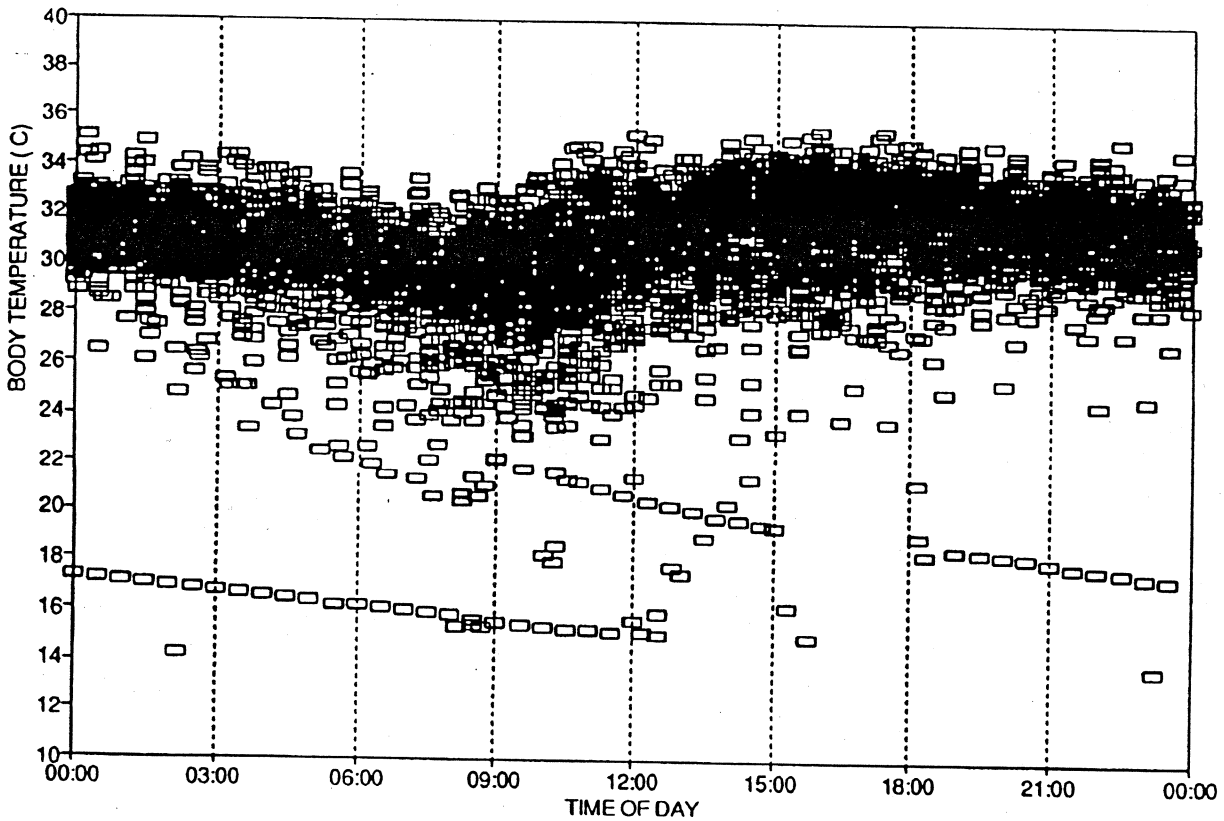

Figure 6. Similarity of daily cycles in body temperature between echidnas throughout the active season, illustrated by pooling all data from ten echidnas, nearly 6000 data points, from February 1987 to November 1989. See text for discussion of several runs of low values.

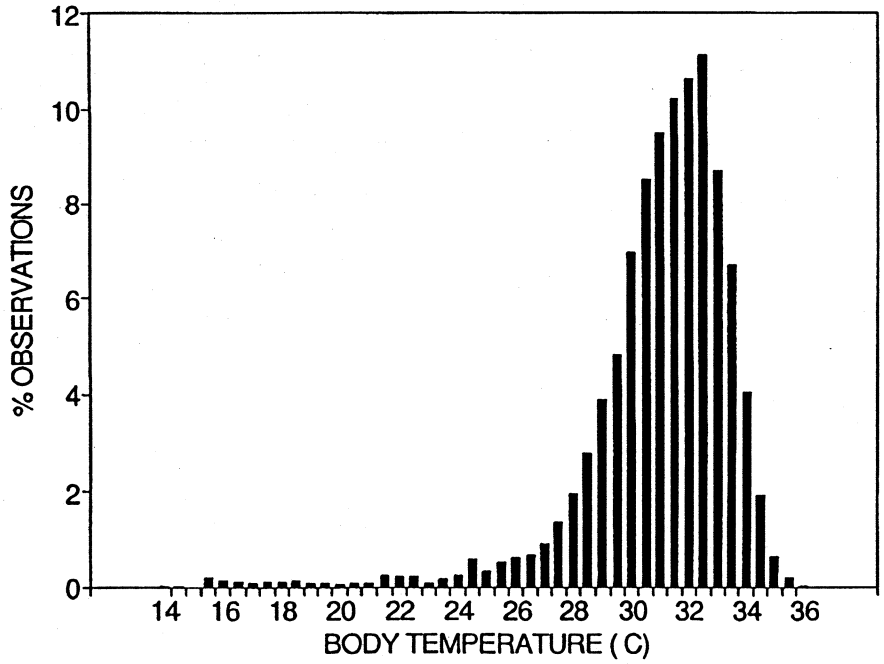

Figure 7. Frequency distribution of all active season body temperatures.

foraged in full sun on an open ridge (Fig. 8 lower panel). T_a had climbed from an overnight low of 10°C to 25°C by late morning and #15's body temperature from 27 to 34°C by early afternoon. Going over the ridge, it moved downslope towards a small creek. Once in the gully T_b fell rapidly, by 2°C in just a few minutes. Presumably, although not seen, the echidna had entered the creek to cool down; no other explanation for such a rapid fall in T_b seems likely, and we have since then twice seen bathing by an echidna on a hot day in southern Queensland.

Opportunities to observe an echidna emerge from its overnight retreat were rare. Hence, information about the possible significance of sun basking in the daily temperature rise is very scarce. One observation was made in late February 1987 when #10 was observed basking in mid-morning sunshine, sheltered by fallen logs and rocks from a gusty wind whose noise assisted by obscuring the observer's approach. T_a was 13-15°C, T_b 28.0°C. The animal lay sprawled, facing away from the sun, with at least one hind foot stretched rearwards. The animal shifted a couple of times to remain in the sun as shadows moved and once rolled onto its back. Body temperature rose only very slowly, 1.5°C in 78 minutes of observation, reinforcing the notion that exercise is the main source of heat for the daily temperature rise. Sun basking in the same posture has been observed in captive animals too.

The low points in body temperature seen in Figures 6 and 7 fall into two categories. Most occur on a day when the individual remained in its retreat, usually in bad weather, and continued to cool right through to the following day (upper panel Fig. 9). Similar-looking events which occurred in February, sometimes lasted 2-3 days and may, by analogy with other hibernators, be described as "test drops" (Strumwasser 1960) prior to entering hibernation (lower panel Fig. 9). Such 'test drops' were often seen in fine, warm weather. They seem to be a routine feature of the thermal pattern; we saw them in all six echidnas for which we had adequate data at the appropriate time of the year.

There was no significant dependence of an individual's daily minimum or maximum body temperature on minimum or maximum ambient temperature (Fig. 10). Further, minimum body temperatures of animals at higher elevations were no lower than those in milder conditions at Waste Point.

Thermal relations of echidnas in their hibernation season

In between periodic arousals, T_b of hibernating echidnas (T_{hib}) falls close to ambient. Hence, hibernation temperature falls progressively as winter advances and rises with the coming of spring (Fig. 2), following the seasonal change of temperature within the hibernaculum.

Measurements of the relationship between T_{hib} and ambient temperature within the hibernaculum were somewhat difficult to gather. Figure 11 presents data from three individuals in which we were able to place an ambient temperature transmitter in close proximity to a hibernating individual. T_{hib} tends to average 1-2°C above the surrounding temperature. Figure 11 shows that they may, however, be from about 4°C above to 1°C or more below ambient temperature. Such situations almost certainly represent non-equilibrium conditions in a hibernaculum where ambient temperature within the hibernaculum goes through a large daily cycle. The lowest T_{hib} we measured was 3.7°C (#10), with a surrounding temperature of 0.8°C.

Hibernation is punctuated by periodic arousals during which T_b rises rapidly but briefly to levels typical of those seen in the active season, prior to rapid cooling again to a level close to ambient (Fig. 2).

Arousal frequency is variable but correlates well with

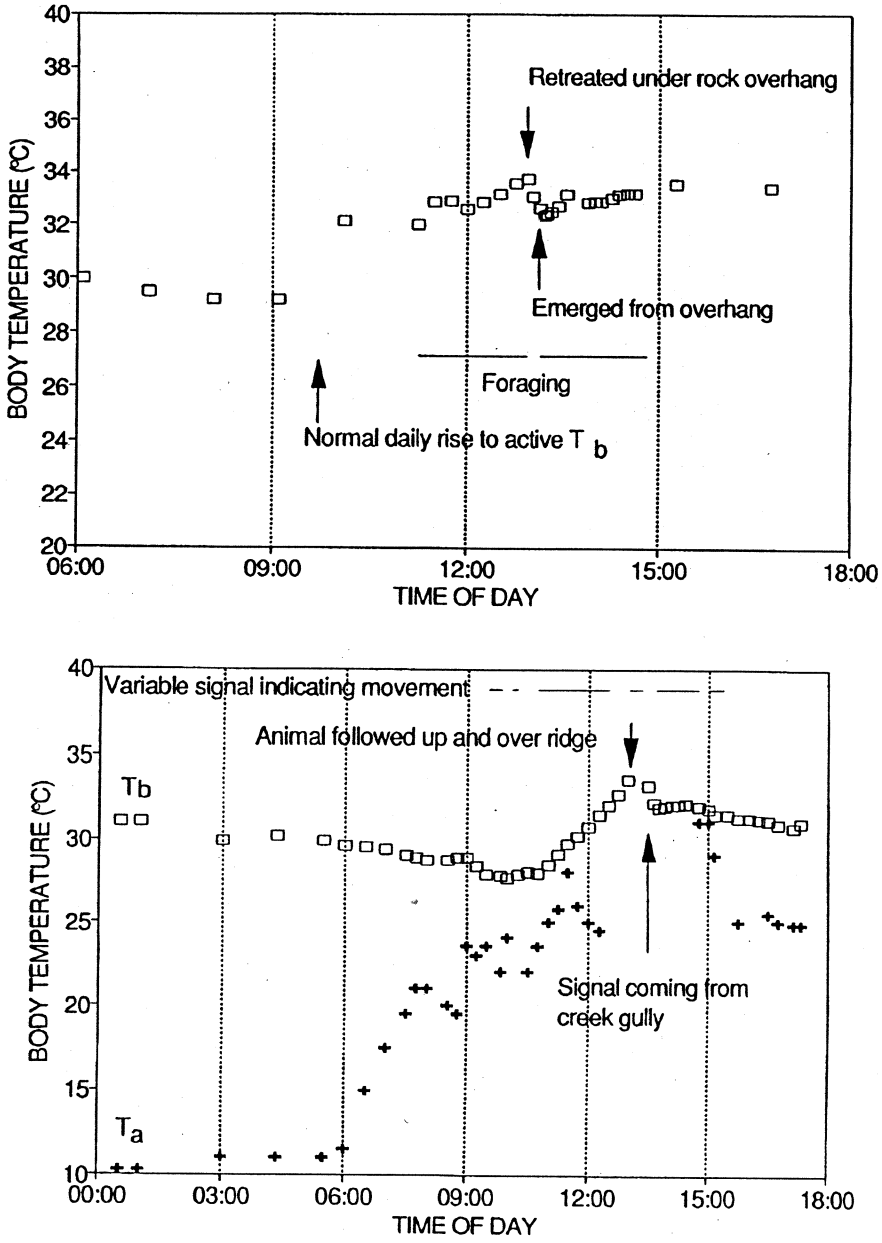

Figure 8. Behaviourally induced cooling by seeking shade and sprawling on the rocky floor of a small cave (upper panel, #12, Dec. 4, 1987) and, by inference, by bathing in a mountain stream (lower panel, #15, Jan. 11, 1988).

T_{hib} immediately prior to the commencement of the warm up. Data from three individuals for which we have a good sequence of data are plotted in Figure 12 and imply warm-ups approximately every seven days at T_{hib} = 15°C and every 28 days at 7°C.

Two typical arousal curves are shown in Figure 13. Body temperature rises at a rate of about 2.4°C per hour and a high body temperature is maintained for 12-24 hours before there is a rapid fall again towards ambient.

In one individual, #30, dug from its hibernation site within a large rotting log, we monitored T_b and watched while it warmed gradually from 12 to 35°C (Fig. 14). Until 18°C, T_b rose without any visible sign of shivering or muscular movement except for occasional slow movements of the limbs and body. Above 18°C occasional body twitches were seen and, at 20°C, shivering commenced and persisted for the remainder of the arousal. Once shivering commenced, the rate of temperature increase steepened. Ambient temperature was 14-15°C throughout.

Changes in body weight throughout the year

As a consequence of our reluctance to interfere with the animals, for fear of introducing handling artefacts in their behaviour, we have fewer data on body weight than we would like. However, a clear pattern emerges from what we have (Table 1). In general, both breeding and hibernation were accompanied by weight losses in every animal for which we have data, 2-3% per month being typical. Large, even spectacular, increases occurred during the non-breeding part of the active season, typically 7-13% per month, with #10 (4.2%) and #15 (1.9%) the only exceptions. Both were from higher altitudes and #15 had made a 5 km journey over a mountain range between the two measurements (Augee *et al.* this vol.).

DISCUSSION

Active season

It is instructive to compare the frequency distribution of *Tachyglossus aculeatus* body temperature during the active season with that of the platypus, *Ornithorhynchus anatinus* (Grigg *et al.* 1992). In both, normal active temperature is 32°C and temperatures above 34°C are uncommon. In echidnas, however, this modal temperature is seen only during periods of activity, T_b falling during periods of rest so that the concept of mean temperature has little value and the "normal" tempera-

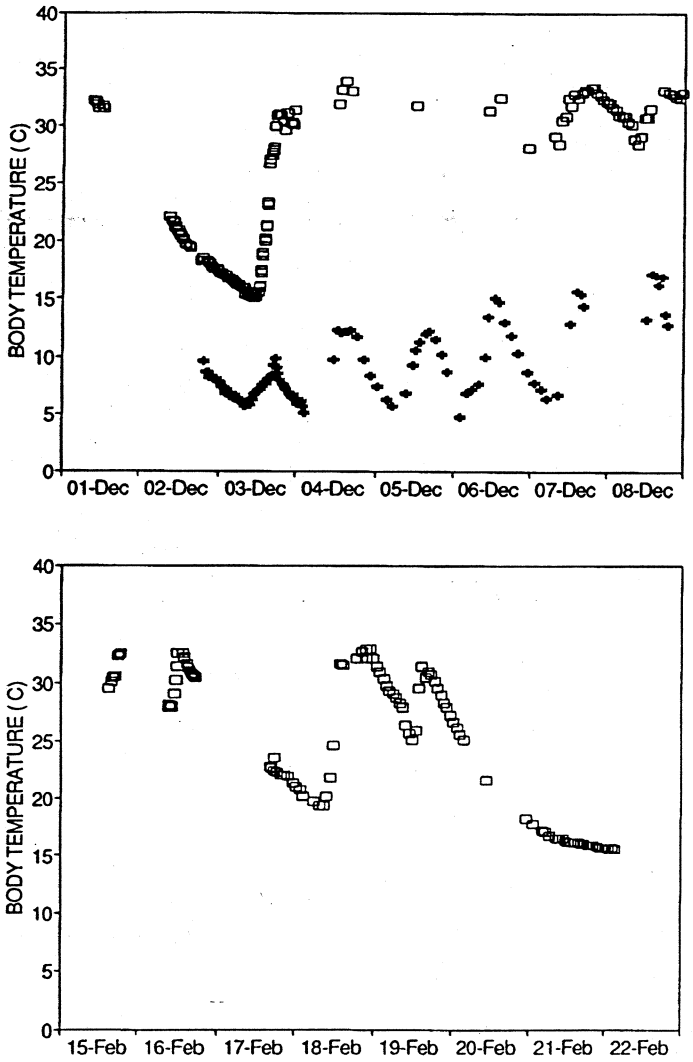

Figure 9. Occasionally in the active season, an echidna remains in its overnight retreat throughout the following day. When this happens, body temperatures may fall much lower than normal as can be seen in theseveral runs of low points in Figures 3 and 4. There seem to be two categories of such occurrences: a "day off", which may be at any time during the active season and is associated with particularly inclement weather (upper panel, #23, December 1988) and a pattern which may be seen in either fine or foul weather and which is seen typically in February (e.g. lower panel, #11, February 1988) prior to entry to hibernation. Such events satisfy the criteria for "test drops" (Strumwasser 1960). #11 appears to have made a "test drop" during 16-18 February, then entered hibernation from 20 February 1988.

ture varies with time of day in a predictable and daily cycle.

In platypuses, however, the frequency distribution is quite symmetrical and 32°C is both modal and mean whether at rest or active (actually 32.06, Grigg *et al.* 1992) and there is no daily cycle. Another difference between the two is the occurrence of low body temperatures. Radiotracking five free-ranging platypuses throughout winter, Grigg *et al.* (1992) found no sign of either torpor or hibernation and only 1.5% of more than 2,000 measurements were lower than 30°C. None was below 24°C. In echidnas, by contrast, leaving the hibernation season aside, 28% of nearly 6000 measurements were below 30°C and temperatures below 29°C were an almost daily occurrence. Temperatures below 24°C occurred in all individuals, and some were as low as 13-14°C. Much lower temperatures, of course, typify the hibernation season.

Echidnas have been portrayed as heterotherms (see Augee 1978) and our data confirm this. However, the persistent day to day similarity of the daily cycle in T_b both within and between individuals throughout the active season (Figs. 5,6) and irrespective of ambient temperature (Fig. 10) and of season shows that, while heterothermic, they are heterothermic in a very controlled way. For animals in Kosciusko National Park, at least, the daily cycle in body temperature has a high degree of predictability regardless of the weather or the ambient temperature. One might expect the extent of the daily fall in T_b, throughout the period of retreat, would correlate with ambient temperature, falling more on cold than warm mornings. This is, however, not the case (Fig. 10). On the other hand, if the animal does not emerge from the overnight retreat to forage on a particular day, T_b continues to fall and temperatures much lower than those typical of the active season are then seen (Fig. 9). Failures by echidnas to emerge mid-morning from the overnight retreat are uncommon and, apart from "test drops", seem to be provoked by foul weather. Echidnas are, however, often out and about in cold, wet weather, their pattern of T_b following the normal daily cycle, and what factors dictate the choice on a particular day are not known. It should be noted as well that disturbance, such as an over-zealous observer, will keep an echidna in its retreat. Also, in breeding females, behaviour associated with care of the young keeps her in the burrow although in this case body temperature remains high (Beard *et al.* this vol.).

Concerning the mechanisms by which the typical active-season pattern is achieved, we have identified at least two behavioural events of thermoregulatory significance; shade seeking and entry to cool water (Fig. 8). The possible role of basking remains enigmatic but the major source of body heat is almost certainly physiological, associated with muscular work, as suggested previously (Augee 1969, 1978). Due to the difficulties of making direct observations of echidnas in the field without disturbing them, we have comparatively few records of

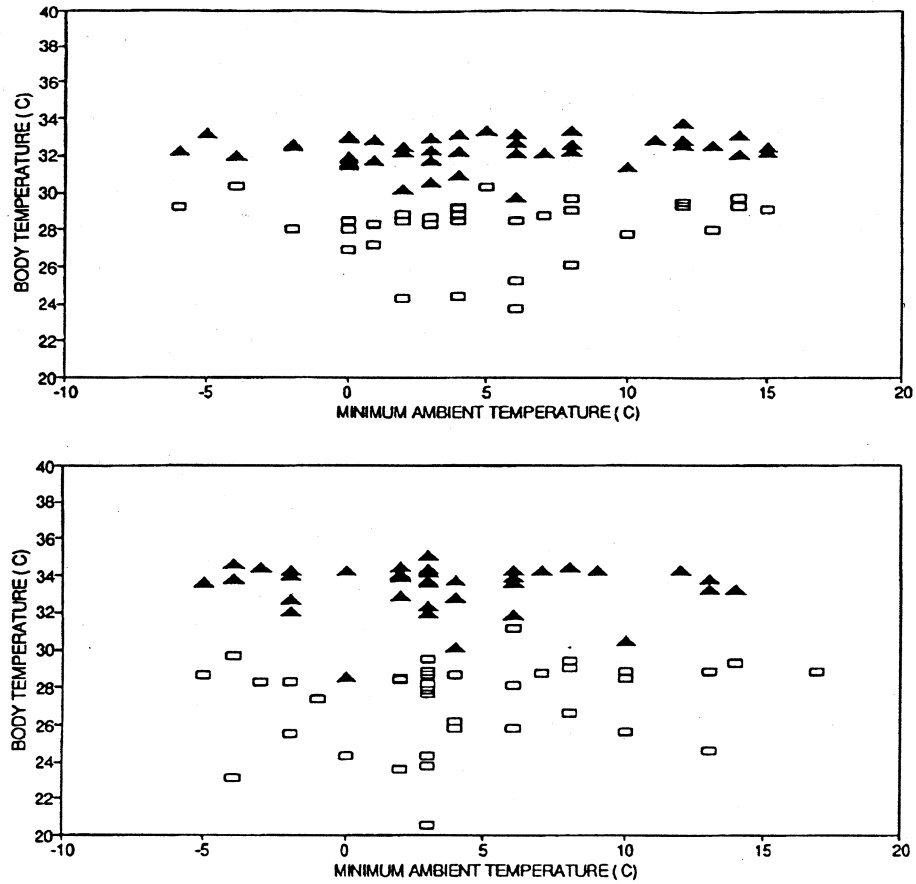

Figure 10 (LEFT). Daily maximum (solid triangle) and minimum (open rectangle) body temperatures of echidnas in the active season are independent of daily minimum ambient temperature (upper panel #13, lower panel #21). Plots against daily maximum temperature (not shown), yielded the same result. Daily ambient maxima and minima were those measured at the Sawpit Creek Ranger Station.

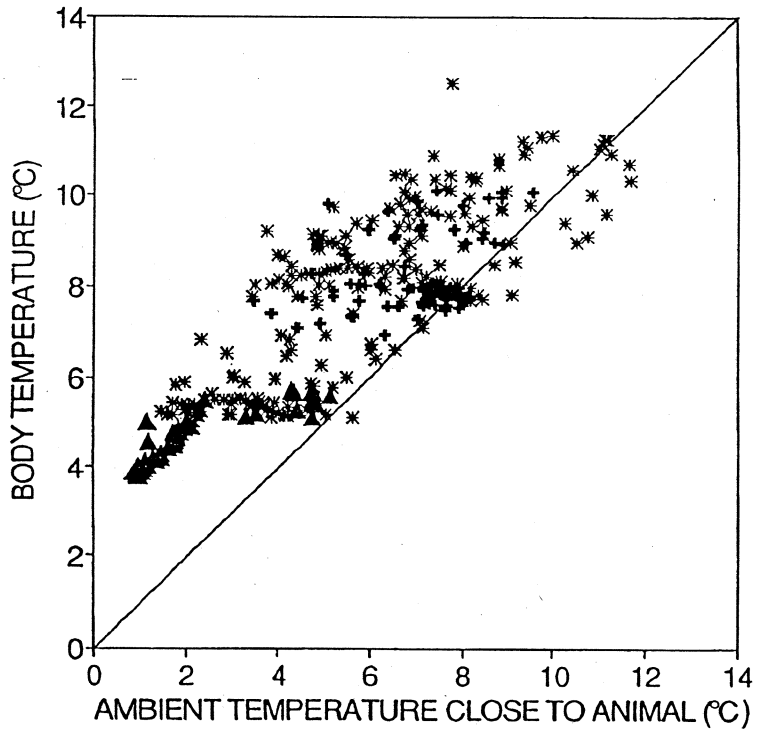

Figure 11. Body temperatures of three echidnas in hibernation, plotted against the temperature measured by a radio transmitter placed within the hibernaculum and very close to the animal (#10 closed triangle, #11 plus sign, #15 asterisk).

the events surrounding the daily emergences from retreats. The data we have, however, suggests that the rapid daily rise in T_b (Fig. 4) begins after, not before, emergence from the overnight retreat and is presumably a result of the muscular activity associated with foraging. Echidnas certainly do bask in the sun, but more work is needed to determine the extent to which basking may be of thermal significance.

There was no obvious daily plateau in body temperature during the active period. Body temperature appeared to rise as the foraging day advanced and fell once the animal (presumably) sought a retreat for the night, producing a somewhat asymmetric, sawtooth pattern of daily changes in T_b (Fig. 4), with a rapid rise and slow cooling.

Echidnas are well known to be poor physiological thermoregulators in the heat, with little or no capacity for sweating (Griffiths 1968, Augee 1978) yet the field data showed successful defence against rises in T_b (Fig. 7), presumably by behavioural mechanisms such as seeking shade or bathing (Fig. 8). We found no

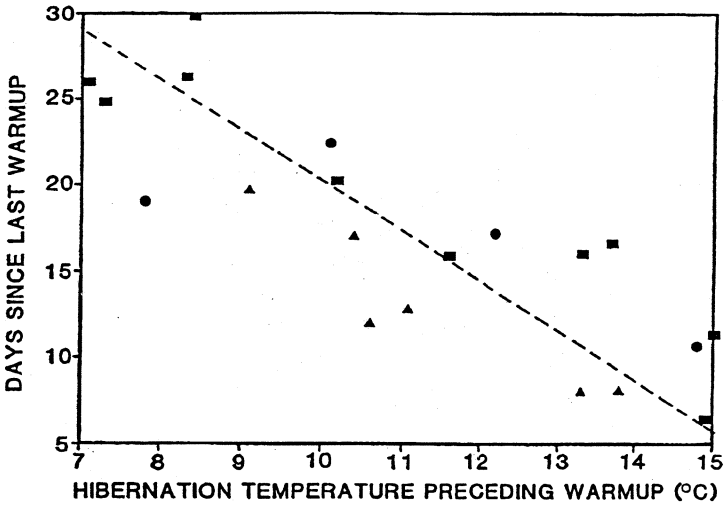

Figure 12. The relationship between the duration of individual bouts of torpor and body temperature just prior to the commencement of the warmup which ends it; data pooled from three individuals; #11 (triangle), #21 (rectangle), #25 (circle).

examples of an animal remaining in its retreat during a hot day, but in other parts of their range echidnas emerge to forage at night, thus avoiding high ambient temperatures (Griffiths 1968, Augee 1978, Grigg, Beard and Fletcher unpublished observations).

In summary, echidnas in their active season in this part of their range show a remarkably consistent and predictable daily cycle in T_b which is essentially independent of the large daily and seasonal variation of ambient temperature.

Hibernation season

No echidna in the study went through a winter without a significant period in hibernation (Fig. 3), extending the observations made in 1987, reported by Grigg *et al.* (1989), when the occurrence of hibernation in echidnas was first described. The finding contrasts markedly with the situation in platypuses in the same cold climate, in which hibernation was not seen (Grigg *et al.* 1992).

Echidnas can be said to be both hibernators in the winter and occasional torpidators at other times. Hudson (1978) has discussed the difficulties of erecting mutually exclusive definitions of the numerous terms applied to the wide range of patterns shown by mammals (and other terrestrial vertebrates, for that matter) in departing from 'normothermia'. Thus, while the terms dormancy, torpor (whether deep or shallow), aestivation and hibernation all convey useful general information about the thermal relations of a species, the diversity of patterns displayed far outweighs the capacity for unambiguous terminology. Nevertheless, in the sense of Hudson, echidnas are 'classical hibernators', becoming torpid for long periods during the winter with body temperatures approaching air temperatures and with infrequent arousals. They are also torpidators; they show periods of shallow torpor during the active season, such as when they remain in the retreat during bad weather and body temperature falls to 14-20°C or so. On the face of it, it seems as though the abandonment of thermal homeostasis comes easily to echidnas, in contrast to the concept of a complex, circannual, tightly programmed series of preparatory changes which are accepted as necessary for hibernation in eutheria. On the other hand, in only very few occasions do the active season torpid events result in body temperatures lower than 20°C. Aloia *et*

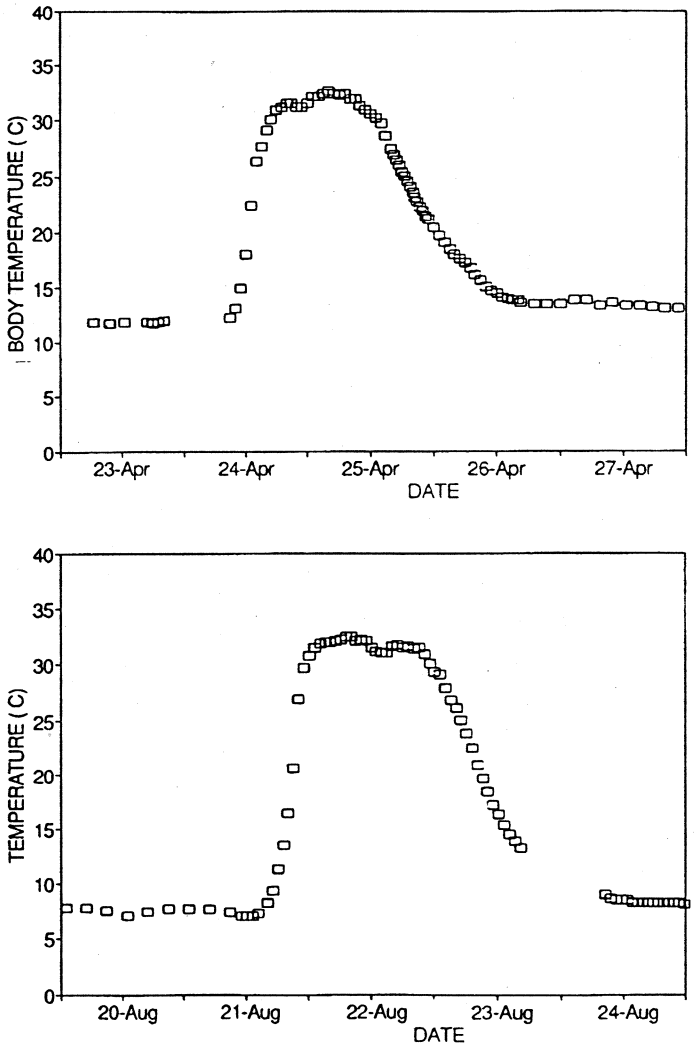

Figure 13. The time course of two typical arousal events (upper #25, lower #21).

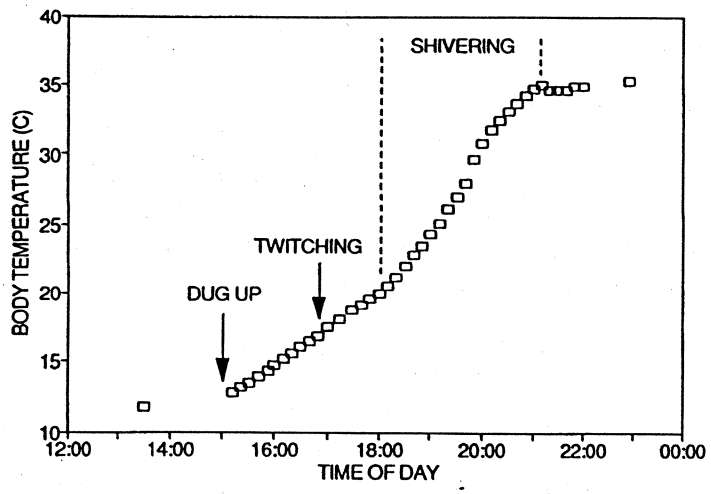

Figure 14 (LEFT). Rate of increase in body temperature in a hibernating individual (#30) after it was dug from its hibernaculum in a log, showing the non-shivering phase of the warm-up below 20°C and the increased rate of warming once visible shivering is initiated.

Table 1. Weight changes during the active season (breeding and non-breeding) and during the hibernation season in echidnas at Kosciusko National Park.

Season		Sex	Animal number	Weight kg (date)	Weight kg (date)	% change	% change per month
ACTIVE	Non breeding	Males	11	4.00 (18/2/87)	4.90 (4/4/87)	+22.5	+15
			13	3.60 (18/2/87)	4.60 (3/4/87)	+27.8	+18.5
			15*	3.55 (18/2/87)	3.65 (4/4/87)	+2.8	+1.9
			21	4.05 (8/11/88)	5.15 (4/3/89)	+27.0	+6.75
			31	3.90 (4/11/88)	5.70 (5/3/89)	+46.0	+11.5
		Females	10*	3.15 (18/2/87)	3.35 (3/4/87)	+6.3	+4.2
			32	4.80 (9/11/88)	6.95 (4/3/89)	+45.0	+11.2
			25	3.90 (2/11/88)	5.90 (3/3/89)	+51.0	+12.75
	Breeding	Males	31	4.35 (21/7/88)	4.25 (20/10/88)	-0.24	-0.8
			11	5.65 (17/7/88)	5.05 (20/10/88)	-10.5	-3.5
		Females	10	3.55 (7/10/87)	3.30 (4/12/87)	-7.1	-3.5
			32	6.05 (17/7/88)	4.80 (9/11/88)	-20.7	-5.2
HIBERNATION		Males	13	4.70 (19/5/87)	4.35 (21/8/87)	-7.0	-2.1
			15*	3.30 (7/5/87)	2.90 (2/11/87)	-12.0	-2.0
		Females	10*	3.35 (3/4/87)	2.95 (18/8/87)	-12.0	-2.7
			12*	3.55 (4/5/87)	2.98 (23/10/87)	-16.0	-2.9
			25	5.90 (3/3/88)	5.20 (22/7/88)	-12.0	-2.7
			32	6.95 (4/3/89)	5.40 (8/12/89)	-22.3**	-2.5**

*

**includes the following breeding season

al. (1986) have discussed the changes in cell membranes which are undertaken by hibernators in the preparation phase for hibernation at body temperatures lower than 20°C. The occurrence of 'test drops' may be related to this membrane reorganisation. The picture which seems to be emerging in echidnas, therefore, is of an animal which easily tolerates periods of shallow torpor in the active season and can enter deep hibernation in the winter. The wide range of entry times and the wide range in durations of hibernation, from 2-7 months, show that echidnas are facultative in their hibernation pattern, unlike the 'traditional' hibernators on whose performances the presently accepted attributes of hibernation have been based. Although the geographic extent of hibernation remains to be delineated, it seems unlikely that echidnas hibernate throughout their range, which reinforces further the concept of echidnas as facultative rather than obligate hibernators.

Echidnas are as large as the largest eutherian hibernators, the marmots. Our largest echidna weighed nearly 7kg, marmots may weigh 7.5kg (Walker 1964). Nedergaard and Cannon (1990) have discussed some of the implications of a large body size for hibernators. On the one hand a larger mammalian hibernator needs to store a lower proportion of its body mass as energy reserves prior to the hibernation season. On the other, the metabolic cost of rewarming to euthermia becomes progressively greater. Nedergaard and Cannon showed that daily torpidity becomes an uneconomic proposition in animals larger than about 10 kg because the cost of rewarming exceeds the energy saving accrued from the period at low temperature. They did not explore the situation for hibernators, but it is interesting to note that echidnas have a lower resting metabolic rate than marmots, yet display a similarly spectacular rise in body temperature with each warm-up, even though they reach euthermia at 32°C rather than 37°C.

The universal occurrence of periodic arousals to euthermia during the hibernation season in rodents, bats and all eutherian hibernators has attracted considerable attention because its functional significance is unknown. Willis (1982) has referred to it as a mystery and so it remains. That it occurs in echidnas also reinforces further the notion that there must be some significant functional benefit. One theory is that arousals are triggered by the need to eliminate metabolic wastes or to restore some metabolite imbalance (Fisher 1964, French 1985). If this is the case, one might expect the frequency of arousals to correlate with hibernation temperature and this has been found to be the case in Golden-mantled Ground Squirrels, *Spermophilus saturatus* (Twente and Twente 1965, Geiser and Kenagy 1988). Our data on echidnas agree very favourably (Fig. 12); the first time that this correlation has been shown under field conditions. This adds support for the notion that the length of torpor bouts in the hibernation season is metabolism-related. Also in support, French (1985), in a study using bats, ground squirrels and marmots, found a good relationship between the number of hours spent in euthermia at each arousal event and body mass. Interestingly, echidnas fit his relationship very well.

There are surprisingly few studies where body temperatures of hibernating species have been followed by radiotelemetry throughout winter. Studies by Wang (1978) on Richardson's Ground Squirrel, *Spermophilus richardsoni*, and Fowler and Racey (1990) on hedgehogs, *Erinaceus europaeus* reported generally similar results, emphasising once again the similarity of the pattern of hibernation in echidnas to the classical mammalian pattern.

The idea is well-embedded in the literature that hibernating eutherians metabolically resist any fall in body temperature below 2-3°C (Lyman 1948). The lowest we found was 3.7°C, at a hibernaculum temperature of 0.8°C. Figure 11, in which the lowest body temperatures appear to break away from the linear relationship of other body temperatures to ambient temperature, suggests active resistance to body temperature falling below about 3°C. However there is unsufficient data to test whether this apparent change in slope is significant. Hibernating echidnas must encounter much lower hibernaculum temperatures than those we measured, and more data are needed before this question can be resolved. In a study of captive individuals in an outdoor pen in Fairbanks, Alaska, Barnes (1989) found that Arctic Ground Squirrels, *Spermophilus parryii*, tolerated body temperatures as low as -2.9°C without freezing and that spontaneous arousals could occur from that temperature. Barnes sounded surprised (p 1594) that his was the first record of sub-zero hibernation temperature, but the lack of prior discovery is probably a reflection of the small number of telemetric studies as much as anything else.

The results of our field studies on echidnas and laboratory studies by Nicol *et al.* (this vol.) show no real difference in details of hibernation between echidnas and the "classical" hibernators. Therefore, if hibernation is an extension of the ability to undergo short periods of torpor, and as echidnas show both torpor and hibernation, it may be reasonable to propose the echidna patterns as a model for the evolution of endothermy. We expect to be addressing these questions elsewhere.

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